OPAL PHYTOLITHS AS EVIDENCE FOR DISPLACEMENT OF NATIVE CALIFORNIAN GRASSLAND

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ABSTRACT

Opal phytoliths are produced by plants and persist in soils as microfossils with taxonomically distinct morphology. We found phytoliths produced by the original native perennial species in soil under an annual grassland, thus providing the first direct evidence that the Californian grassland was formerly dominated by panicoid opal-producing grass. The most common panicoid-type opals were probably produced by *Stipa pulchra.* Frequencies of opal phytoliths from native grasses were greater at 10 cm depth than at the soil surface beneath the annual grassland. Comparison of opal phytolith frequencies from 10 cm deep at the annual site and an adjacent relict perennial grassland site suggested that the density of panicoid opal-producing native grasses on the annual site was once similar to the relict grassland.

Reconstruction of pristine plant communities in California is constrained by limited techniques for establishment and maintenance of natural vegetation, and by a lack of recorded knowledge about the composition of those historical communities. The evidence for previous vegetation includes results from pollen studies, macrofossils, observation of succession, and the composition of present vegetation on selected relict sites. One technique, which has not been applied to any California plant community, uses opal phytoliths to identify historical species assemblages.

Plant opals are microscopic, translucent particles that occur in plants and persist for long periods in soil as opal phytoliths. They are formed within plant cells and cell walls through the passive uptake of monosilicic acid by way of the transpiration stream from soil solution (Jones and Handreck 1967). They are composed of amorphous silica, which also contains some additional carbon, water, and cations (Wilding et al. 1975). Opals are most common in leafy portions of plants but are also present in stems, roots, and other parts. Biogenic opal particles range in size from less than one micron to over 500 microns; however, the majority of diagnostic forms range from two to 50 microns.

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Research on opal phytoliths initially emphasized investigations of biogeochemical processes, genesis of paleosols and of catenas, and loess deposition, in which phytoliths were studied as components of soil (Wilding et al. 1975, Twiss et al. 1969, Moore 1978). Plant ecologists and paleoecologists have now begun to use phytoliths to document vegetation change, post-glacial succession, type distributions, and shifting ecotones such as grassland-forest boundaries (Wilding et al. 1975, Moore 1978, Rovner 1983, Palmer 1976).

Plant anatomists refer to opals as "silica bodies" or "silica idioblasts." They are useful in taxonomic descriptions and have been useful in classification of monocots (Metcalfe 1960). Members of the Poales (grasses and sedges) have a significant propensity to form opals. In the Poaceae (Gramineae), silica body morphology is considered diagnostic at the subfamily and tribal levels. There are at least three recognized types of silica bodies in grasses: festucoid, panicoid, and chloridoid (Twiss et al. 1975), which suggests a correlation between opal cell morphology and C3 and C4 type photosynthesis (Rovner 1983, Palmer 1976).

These taxonomic affinities are useful to differentiate Californian grasses. The common grasses that now dominate the Californian grassland are festucoid species introduced from the Mediterranean (Heady 1977). Native perennials assumed to have dominated the pristine grassland, *Stipa* spp. and *Danthonia californica* Boland., contain significant amounts of panicoid opals (Barkworth 1981, DeWet 1956, Bartolome and Gemmill 1981); others, including the genera *Deschampsia* and *Distichlis,* are exclusively festucoid. The typical "dumbbell" or "hourglass" shape of panicoid opals is readily distinguished from the elliptical disc or "hat"-shaped festucoid types and from silicified, dumbbell-shaped, stomatal guard cells (Figs. 1a, 1b). Several distinctive types of silicified trichomes (unicellular or bicellular hairs) also are associated with particular tribes or genera (Metcalfe 1960, Barkworth 1981, DeWet 1956).

This paper describes the use of opal phytoliths from two soil depths to document replacement of native vegetation by exotics on Jepson Prairie Reserve in Solano County, California (Lat. 38°N, Long. 122°W), 75 km northeast of San Francisco. The Prairie contains a small remnant of the California Valley Grassland or California Prairie, which may have covered much of the Central Valley (Heady 1977). The vegetation on all but a few hectares of the 1000 ha reserve, described in detail by Barry (1972), is now dominated by annual grasses from the Mediterranean region.

Study Sites

The study contrasted two locations. One location is dominated by native grasses and forbs, including *Stipa pulchra* Hitchc. and

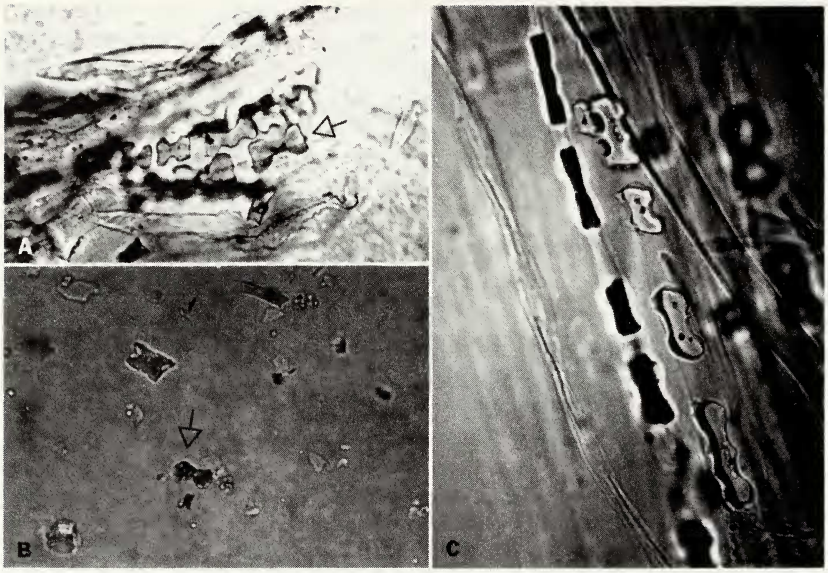

FIG. 1. Photomicrographs of opal phytoliths. a. Dumbbell-shaped panicoid opals (length = 25 microns), isolated from leaf tissue of *Danthonia californica*, are visible in the center of the photomicrograph. b. Opal phytoliths isolated from annual grassland soil, 10 cm depth (480× magnification). The arrow points to a phytolith produced by a perennial, *Stipa pulchra*. c. Linear arrangements of panicoid opals (length = 20 microns) in leaf tissue of *Stipa pulchra*. Dark rectangular shapes are opals viewed on edge.

Deschampsia danthonioides (Trin.) Munro ex Benth. This pasture has been grazed lightly by sheep for at least the last 100 years. Stands of *S. pulchra* averaged 4.2 plants/m^2 when sampled in the spring of 1985 on 30 permanently marked 25 cm × 25 cm plots (B. Leitner, pers. comm.). Frequency of *S. pulchra* measured 23.3 percent on these same plots, with the remainder of the vegetation exotic and native annuals. This density is typical of relict non-coastal sites (Bartolome and Gemmill 1981).

The second pasture also is part of the Reserve and is less than one km away, but it has been in different ownership and grazed by cattle. Annual grasses of Mediterranean origin, including the genera *Bromus, Avena, Vulpia,* and *Hordeum,* dominate the second location. It contains no native tussock-forming bunchgrasses and only a few scattered plants of rhizomatous *Distichlis spicata* (L.) Greene. The nearest native bunchgrasses are 200 meters from the second sample location. The soils are similar, sandy loam or loam derived from sedimentary alluvium, and classified as Palexeralfs or Natrixeralfs. "Hogwallow" or mima-mound topography with vernal pools typifies undisturbed portions of both the sites.

TABLE 1. RATIO OF DUMBBELL OPAL PHYTOLITHS PRODUCED BY NATIVE PERENNIAL GRASSES TO TOTAL OPAL PHYTOLITHS FOR SOIL SAMPLES FROM THE JEPSON PRAIRIE AND FREQUENCY OF FIELDS WITH DUMBBELL OPAL. Sample size numbered 400 from each depth and location. Numbers in parentheses are 95 percent confidence intervals for each value from binomial distribution.

	Annual grassland		Perennial grassland	
Depth	Ratio	Dumbbell opal freq.	Ratio	Dumbbell opal freq.
Surface	0.056 (0.03–0.08)	0.45 (0.39–0.51)	0.154 (0.10–0.19)	0.89 (0.85–0.92)
10 cm	0.144 (0.10–0.18)	0.75 (0.70–0.80)	0.169 (0.13–0.22)	0.80 (0.75–0.84)

METHODS

In August 1984, we collected soil from the surface (0–1 cm) and from 10 cm depth at ten randomly located sites in each of the two locations. Collected samples were air-dried, and the gravel and organic debris removed. The five to 10 g of fine material remaining was sieved through 240 micron mesh plankton netting (Cwynar et al. 1969). Organic matter was removed using 30 percent hydrogen peroxide. Mechanical shaking in a sodium hexametaphosphate (0.5–1 molar)–sodium pyrophosphate (10%) solution dispersed aggregates. Dispersed soil was then wet-sieved through 107 micron mesh plankton netting. Microscopic inspection of coarser material verified that essentially all the opal had passed the sieve.

Particle sizing was performed by sedimentation and decantation using standard procedures (Jackson 1979) adjusted for specific gravity of opal (2.2 g/cc). Soil smears were prepared from a dilute, ammoniated soil/water suspension (Smithson 1961) and placed onto a standard microscope slide and mounted in cedarwood oil. Separate microscope counts were made on the medium silt (5–20 microns) fraction, at 400× magnification using a 0.2 × 0.4 mm grid system. A maximum of 50 fields/slide were used to record frequency of distinctive dumbbell phytoliths, tallied as ratio of dumbbell to total phytoliths.

RESULTS AND DISCUSSION

Dumbbell opal phytoliths, which could have been produced only by native grasses, were, as expected, more frequent in the surface soil of perennial grassland than of the annual grassland (Table 1). Dumbbell opals were nearly as frequent in the annual site subsurface soil as in the perennial site subsurface. Most of these opals are probably from *Stipa pulchra*. The low density of panicoid phytoliths in the surface of the annual grassland site apparently resulted from the replacement of native perennials by introduced annuals and the influx of non-panicoid opal.

Although the replacement of the native grassland by introduced species has been widely hypothesized (Heady 1977), using circumstantial sources of evidence such as the presence of relict stands of natives in presumed undisturbed sites, this study has produced the first documentation of replacement based on more direct evidence. The annual site apparently had a cover of native perennial bunchgrass vegetation. Since settlement by people of European origin, the bunchgrasses were replaced by introduced annuals on the present annual grassland site. Number and composition of panicoid-type phytoliths (Fig. 1c), including some "fan"-or "keystone"-shaped forms (Wilding et al. 1975, Metcalfe 1960) at 10 cm depth, suggests that the present perennial grassland site is similar to the original grassland in density of panicoid opal-producing native bunchgrasses.

Phytoliths show much potential as a tool to study historical changes in vegetation. At the Jepson Prairie, we were able to characterize vegetation change from a grassland dominated by perennial species, which produce panicoid-type phytoliths, to an annual grassland without panicoid opals. We were able to take advantage of a situation ideally suited to the use of opal phytolith characteristics. In other vegetation types, the changes will be more difficult to detect. However, even where the types of opal phytolith produced do not change at detectable levels, the relative abundance of opal in soil can be a useful diagnostic aid. Changes most likely to show large differences in the quantity of opal in the soil occur on grass/shrub or grass/tree boundaries because of the great difference in opal production between grasses and woody species. The invasion of meadows by trees, for example, should be readily detectable with opal phytolith studies. Because of the complementarity of pollen and opal phytoliths (the two tend to differentiate into taxonomic categories differently) and the different dispersal potential of phytoliths, the dual use of phytoliths and pollen for studies of vegetation history should increase.

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